Nixon, E.L

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FIRE BLIGHT

IMPERIAL BUREAU
28 FEB 1929
OF MYCOLOGY

An old orchard in Centre County, Pennsylvania, planted in 1846 and propagated on native root stock. Not a tree has died from root trouble.

THE PENNSYLVANIA STATE COLLEGE
SCHOOL of AGRICULTURE and EXPERIMENT STATION
STATE COLLEGE, PENNSYLVANIA

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FIRE BLIGHT*

E. L. Nixon

Cause of the Disease

FIRE BLIGHT OF THE POME FRUITS is a germ disease, which is caused by the bacterium, *Bacillus amylovorous*. Bacteria are extremely small organisms which are known chiefly because of their connection with disease. Bacteria are so small that they can be seen only when they are examined under a very high powered microscope. They are living organisms which cause disease and death of the tissues of other organisms in a purely incidental way. Even the death of the plant or animal attacked is merely an incident in the attack of the bacteria.

In attacking a plant or an animal, the bacteria are concerned only with obtaining the necessary food for their own life activities. That bacteria secure this food at the expense of another living organism is merely incidental. This sort of existence is what is called "parasitism." Low forms of living organisms, such as bacteria, fungi, and even very low forms of animal life, become very highly specialized in this mode of existence. In some cases they become so highly specialized that they are able to live on but one kind of organism.

The *Bacillus amylovorous* attacks the tissue of the apple tree and other pome fruits to get food for itself and to have a place in which to live and to multiply. That the twig or tree dies is probably the greatest calamity that can befall the bacteria, for the death of the twig also means the death of the bacteria occupying those tissues. When once the bacteria causing fire blight have gained entrance into the apple tree, they continue their growth and multiplication regardless of external conditions, such as rain or sunshine, heat or cold, so long as the conditions within the plant remain favorable for their growth. Winter conditions cause the bacteria to go into a dormant or resting state but do not kill them, as is seen by the occurrence of the disease year after year in the same orchard.

History of Early Speculations as to Causes of Fire Blight Disease

Since twig blight is the most conspicuous form of the fire blight disease it was naturally the first to be observed. Twig blight has been recognized and described for over a hundred years. The theories as to the cause of fire blight of the pome fruits are numerous and, to say the least, interesting, for they are in keeping with contemporary theories as to the causes of diseases in general. Some

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Appreciation of suggestions and criticism is extended to the members of the Botany Department of The Pennsylvania State College and particularly to Dr. J. Ben Hill.

FIG. 1—BLOSSOM BLIGHT

This frequently involves the entire blossom cluster and fruit spur. The limb at the base of the fruit spur, girdled by the fire blight organism, causes death of the upper portion of the branch. Photograph by L. M. Marble, Canton, Pennsylvania.

of the earlier conceptions as to the cause of fire blight may be of interest in this connection.

A number of the early writers attributed the disease to several causes acting together. Coxe, who described fire blight in 1817, thought "that the hot rays of the sun acting through a misty or saturated atmosphere deranged the vital activities of the plant and brought about the disease." The insect theory arose as a result of confusion with the blight resulting from the attacks of the blight beetle. Several writers independently developed what was known as the frozen sap theory. According to this view, the freezing of unripe wood produced a poison which the moving sap distributed in the spring and which caused the characteristic symptoms of the disease. Even at the present time the effect of fire blight on the roots of the apple is attributed to winter injury. A fungus theory was presented first in 1863 but was never well established. Since blighted trees often attract attention immediately after a thunder storm, the belief arose that the disease was due to electricity, but this argument has never been connectedly presented. It was not until 1879 that Burrill definitely proved that fire blight is caused by bacteria.

Knowledge of the existence of living organisms as small as bacteria was of necessity forced to await the perfection of the microscope. In 1660, Leeuwenhoek, a Dutch grinder of lenses, perfected a microscope sufficiently powerful to render yeast cells and bacteria visible. After Leeuwenhoek's discovery of bacteria some medical men of the time suggested that contagious diseases were due to microscopic forms of life that "passed from the sick to the well," but this doctrine was not well received and gradually disappeared. In the eighteenth century, Plenciz, an Austrian, called attention to the connection between micro-organisms and some diseases, and he advanced the opinion that each disease has its own casual agent which multiplies enormously in the diseased body. But, in spite of the acute reasoning of Plenciz, an astonishingly slight impression was made on the medical thought of his day. This illustrates the futility of the most penetrating speculation when it is unsupported by experimental data.

The real advancement of the subject came in 1837 when de la Tour, Kützing, and Schwann showed that the yeasts which cause fermentation were living things. And very soon after this Schwann and a botanist, Schleiden, advanced the cell theory of living matter. With such a limited knowledge of the subject, it is not astonishing that the cause of fire blight of pear and apple for nearly a hundred years was attributed to so many causes. As in the case of the philosopher mentioned above, acute reasoning alone did not get anywhere for one man's opinion was as good as another.

Not until 1877, when Koch and Pasteur showed the connection between certain microscopic forms of life and the disease of splenic fever which attacks sheep and cattle, was the germ theory of disease actually demonstrated. Two years later, when Professor Burrill reported the discovery of *Bacillus amylovorous* as the cause of the fire blight of pear and apple, knowledge of the first bacterial disease of plants was established.

About this period other notable discoveries were made in quick succession. In 1880 the typhoid bacillus was found, and also the bacillus of fowl cholera. The next year, Koch reported the discovery of the tuberculosis bacillus and, in 1883,

the germ that produces Asiatic cholera. Thus, in a period extending over about fifteen years, the causes of a majority of the infectious diseases were discovered. To-day there is scarcely a person who can read or speak the English language who has not some conception of bacteria and the diseases they cause, and most all have some knowledge of the useful ones like those causing the clover nodules and those of use in dairy manufacturing.

External Features of the Disease

As is quite generally known, fire blight occurs in the following forms:

(1) Blossom blight, which may involve the entire blossom cluster or fruit spur, and which more rarely, may girdle or form cankers on the adjacent larger limbs (Fig. 1).

(2) Twig blight, including water sprout infection which is often responsible for the formation of hold-over cankers. Most of the water sprout and twig infections die out, however, before forming hold-over cankers (Fig. 2).

(3) Canker blight, which is frequently a hold-over form in which the bacteria

FIG. 2.—TWIG BLIGHT ON "WATER SPROUTS," AND BLIGHT-INFECTED ROOT

The two twigs were inoculated directly from the root. The root shown in this figure was taken from the experimental orchard at The Pennsylvania State College.

live over winter. Cankers usually occur at the base of water sprouts, fruit spurs, or small limbs, through which the blight organism entered to form the canker (Fig. 3).

(4) Collar blight, which in reality is a hold-over canker form located on the collar or at the base of the tree. (See Pennsylvania Station Bulletin 136, "Collar Blight and Other Related Forms of Fire-Blight," by Orton and Adams, published in 1915).

(5) Root blight, which most often is a hold-over form (Figs. 4 to 9). These last two forms are the most destructive of all for they frequently cause the death of the entire tree.

Blossoms are infected at full bloom when bees and other insects gather nectar. Probably these insects distribute the bacteria from exudating hold-over cankers and from infected to uninfected blossoms. If the seasonal conditions are such that hold-over cankers are exuding copiously during the blossoming period, severe epidemics of blossom blight may occur. But fruit growers seldom observe blossom blight infections in the very early stages, for not until the flowers and the young leaves on fruit spurs are dead is the disease readily detected (Fig. 1). Confusion also results because blossoms may die from causes other than fire blight and the grower may find it difficult to determine whether late frosts, lack of pollination, mechanical injuries, such as spray injury, or fire blight cause the death of the blossoms. The death of the blossoms by fire blight occurs several days after the infection has taken place and after the bacteria themselves have run their course through the tissue. Blossom infection occasionally occurs with such severity that it interferes with the set of fruit. The most serious damage is done, however, in the secondary infection of adjacent twigs and branches leading to the formation of hold-over cankers and to the development of the large masses of bacterial exudation for further infection of other parts.

From this new source of bacteria other adjacent tissues and regions are directly invaded and still other infections take place. Young growing shoots and water sprouts are the most frequent places in which to observe infection. Once a tree is badly infected it appears as though the leaves had been scorched by flames and, from this appearance, the name "fire blight" has arisen. Almost everywhere on the surface of such dead and dying parts, including leaves, leaf petioles, the young succulent twigs and fruits, droplets of a clear or amber-colored exudate may be observed. This exudate is a jelly-like substance filled with innumerable bacteria.

Since it is very soluble in water, rains may dissolve it, washing the bacteria down to the soil where they may infect the roots. It is possible that the infection takes place through injury from many causes and the disease becomes established in the root system as root blight. (Fig. 4.) The roots also may become infected through sprouts that spring from the base of the tree. Root blight is the most destructive form of all the phases of fire blight, for the tree is killed outright or so badly injured that it is no longer profitable.

Since fire blight is known to enter growing tissue only through wounds, it is called a wound parasite. These wounds may be produced mechanically by insects or by cultivating tools or pruning instruments or they may be growth cracks. The delicate tissues of the blossoms, however, are an exception, for they

FIG. 3.—CANKER BLIGHT ON TRANSCENDENT CRAB

This is the form in which the disease lives over winter. This so-called "holdover canker" was collected in zero weather and furnished material for microscopic preparations which revealed the encysted condition of the blight organism. This specimen was collected in Chester County, Pennsylvania.

furnish a natural entrance without injuries. It is not the intention here to go into a long discussion of the gross features of the disease. Superficial observations of the fire blight disease have often been the topic of discussion in horticultural meetings. Because fire blight is such an important disease of the pome fruits and because its external effects are so conspicuous, probably more has been written and spoken on the subject than on any other plant disease. These phases are well known to fruit growers.

Results of Investigations

While the symptoms and the superficial aspects of the fire blight disease are well known, the exact nature of the disease and the behaviour of the bacteria causing the disease can only be determined by the use of the microscope. When the present investigations were first undertaken it was found best to introduce the bacteria into the tissues artificially. This method made it possible to study the progess of the disease from its very beginning. Fire blight bacteria were grown in pure culture (that is, free from other organisms) and inserted into the

FIG. 4.—ROOT BLIGHT ON 9-YEAR-OLD STAYMAN

This is commonly a "hold-over" form. It is a very destructive stage of the disease. This specimen was collected in Luzerne County, Pennsylvania, in 1918.

young apple twigs by means of a small needle. The trees thus treated developed the typical symptoms of fire blight. That such minute organisms as bacteria can affect plants (and animals) so disastrously is rather astonishing until one appreciates how they migrate in the tissues, how they procure their sustenance from the plant, and what effect these operations have upon the cells of the afflicted plant.

To show how the bacteria migrate in the tissue, little blocks containing the puncture made by the needle in introducing the bacteria were cut from the twig. In order to see through them with the microscope and observe just how the bacteria

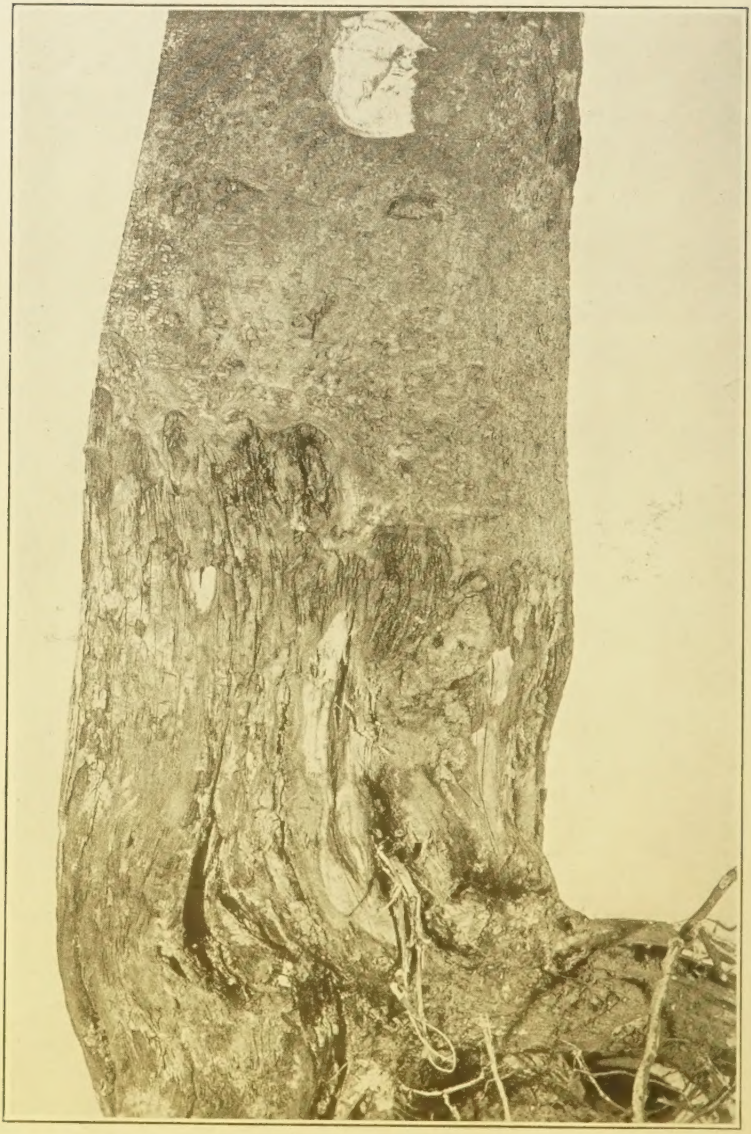

FIG. 5.—THE DEADLY WORK OF ROOT BLIGHT

This is a "close-up" of the specimen in Fig. 4, showing the sharp line of demarcation between dead and living tissues at the junction of the "French Crab" stock and the Stayman scion. The mark near the top indicates the ground line.

FIG. 6.—SAWED SECTION REVEALS ROOT BLIGHT

The specimen, shown in Figs. 4 and 5, was sawed to show the union of stock and scion. This is the reverse of Fig. 5. It clearly illustrates that it is a budded tree. By detailed study of Figs. 5 and 6 it is seen that the blight organism stops its invasion upon reaching the more resistant tissue of the scion. Only the stock has been killed.

lay in the tissue the blocks were cut into sections almost as thin as the bacteria themselves.

For a proper appreciation of the effects of the fire blight organism on the tissues of the apple, the structure of the young twigs must be understood. The young twigs grow in length at the tips. A microscopic examination of the extreme tip of the twig shows this tissue to be composed of cells all exactly alike, but a little back of the tip the tissues are made up of different kinds of cells (Fig. 15). The tissues which can be recognized are the pith (Fig. 15A) in the center, the young wood region (Fig. 15B) outside the pith, and the growing layer or cambium cylinder (Fig. 15C) just outside the wood. The soil moisture taken in by the roots is carried upward through the wood layer to the very tips of the branches. Just outside the cambium layer is a layer of tissue called the phloem (Fig. 15D) which functions in carrying food materials from the leaves downward through the twigs, branches, and stems to the roots. On the extreme outside of the very young twig is a single layer of cells called the epidermis (Fig. 15G) which protects all the other tissues from drying out. Between the epidermis and the phloem is a tissue called the cortex (Fig. 15E).

It is in this cortex that the fire blight bacteria first start to multiply and in which they make their most rapid progress through the twig. In sections taken from material about one hour after the punctures were made, the bacteria were observed imbedded in a jelly-like substance along the edge of the puncture (Fig.

FIG. 7.—ROME BEAUTY GRAFTED ON FRENCH CRAB SEEDLINGS

These specimens were taken from trees whose roots had been inoculated. All were killed in one season. Left to right, 1-year-old, 2-year-old, 5-year-old. It is clearly evident that the method of propagation is by piece-root grafting.

FIG. 8.—REVERSE VIEW OF FIG. 7

Five-year-old tree, showing death restricted to the "French Crab" stock while the more resistant Rome Beauty scion remained uninfected. The fire blight bacteria were recovered six months after inoculating where the bark is removed at the lower right hand corner.

16A). Later stages of material showed that this bacterial mass becomes larger and larger until occasionally the entire puncture made by the needle is filled with bacteria imbedded in the jelly. The beginning and continued growth of this bacterial mass is always in this cortical region.

The cortex has the function of acting as a special storage tissue for the excess food material made in the leaves, and the cells which compose it have thin walls and comparatively large spaces between them. Through these intercellular spaces (Fig. 16B) the jelly-like substance containing the bacteria creeps along from the margin of the puncture caused by the needle. The movement through the tissue is comparatively rapid, so that by the time the horticulturist has first observed the effect of the bacteria, as manifested by death of the twigs, the organisms have migrated down the limb as far as they will go. In this early migration stage in the cortex, the bacterial mass, even though it completely surrounds the cells, has no apparent ill effect on them. The spaces between the cells are used as a pathway for the migration until finally the bacteria becomes so numerous and so fill the spaces between the cells that sufficient pressure is developed to separate one cell from another; at the same time the cells themselves begin to shrivel and shrink, and the death of the tissues slowly takes place.

FIG. 9.—BARK HARBORS BACTERIA

The piece of bark pictured above is the one referred to in the legend of Fig. 8. This shows the mass of fire blight bacteria extending from the bark out over the culture medium.

FIG. 10.—NINE-YEAR-OLD STAYMAN AFFLICTED WITH ROOT BLIGHT

The entire "French Crab" stock is dead. The life of the tree was saved by the timely development of a root from the tissues of the Stayman scion. The specimen was collected in 1917.

By this time large cavities filled with bacteria appear in the entire cortical region (Fig. 16C). This may be called the vegetative stage of the fire blight organism. In this manner the organism distributes itself widely through the tissues of the plant. At this stage of the development of the organism within the tissues, the characteristic external symptoms (Figs. 1 and 2) begin to manifest themselves. The whole twig, with its leaves begins to take on the typical scorched appearance. While microscopic examination shows the first symptoms of death of individual cells within 48 hours, the external appearances of death do not begin to manifest themselves until four or five days after the bacteria have been introduced (Fig. 16A). Under such conditions as described above the bacteria always disintegrate; that is, the masses of bacteria that occupy these large cavities (Fig. 16D) formed among the cells are unable to live through adverse conditions and reproduce the disease the following season. This is why infected blossoms, twigs, and even small limbs which have been killed do not play an important part in reproducing the disease the following year.

As this jelly-like mass of bacteria is observed migrating down the twigs to older limbs, a change of the bacteria in shape and size occurs. In addition to this they acquire the ability to dissolve the cell walls (Fig. 16C) of the apple tissue and enter and destroy the living cells. This results in the formation of large cavities deep in the tissues of older limbs or of the body of the tree itself. Contrasting these cavities with those referred to earlier, the following differences are in evidence:

In the former (Fig. 16D) the cavities are formed by splitting the cell walls partly by pressure of the bacterial mass and partly by a shriveling of the wall or a withdrawal of the cell contents. There is never any suggestion of the bacteria

FIG. 11.—LAYERING, A METHOD OF PROPAGATING TREES ON THEIR OWN ROOTS

Over two hundred young trees were taken from this tree. Only the terminal bud of each limb should be left exposed.

entering these cells or any visible effect on the cell walls such as their dissolution. In the latter, there is no indication of large bacterial masses in the spaces or any indication that pressure is being exerted (Fig. 16C). The bacteria gain a ready entrance into the cells and ultimately destroy the living cell contents and also the cell walls. Areas may be seen in which the destruction of several cells has resulted in extremely large cavities.

Whether these changes in the size and abilities of the bacteria are reactions to physiological changes of the host tissues or are inherent changes in the life cycle of the bacteria has not been determined. About all that can be said is that all of the changes enumerated always take place between the times of infection and "hold-over" canker formation.

Of the small number of canker formations (Fig. 3) on the larger limbs resulting from twig and blossom infections, only a small percentage is found to be hold-over cankers, that is, areas in which the bacteria live over until the next season and thus reproduce the disease. It was found that the death of many of the areas on the larger limbs is produced in the same manner as that of the young twigs and fruit spurs; and as in these cases, the bacteria die out very quickly after the death of the host tissue (Fig. 16D).

In other cases the bacteria, either in response to stimuli from the host tissue or as an inherent change in the life cycle of the organism, enter the cavity of certain cells and there round up into masses or cysts (Fig. 16E), the form in which they survive the adverse conditions of winter. The bacteria in this encysted condition withstand excessive drying and intense sunlight, two conditions very destructive to them in their vegetative condition.

In the spring or on the occasion of renewed growth or sap flow, these cysts take up moisture, swell to several times their former size, burst out of the cells, and, joining those from other cells, migrate outward to the surface where they appear as the well-known canker exudate. Here it serves as a source of infection for the blossom blight again. Canker exudation completes the normal cycle of development from infection to infection, which under natural conditions covers a period of one year.

The results of this investigation indicate quite clearly the following:

(a) Recommendations for Control

1. That where fire blight is troublesome a system of culture or fertilization restricting growth to a conservative or controlled degree may be adopted which will render the trees less susceptible to the disease. Any system of culture or fertilization which stimulates excessive growth not only renders the tree more susceptible to the disease but renders the attack more severe. Nitrate of soda or sulphate of ammonia due to their more rapid absorption and consumption are better sources of nitrogen than barnyard manure since these promote a shorter growth period. After the terminal buds have formed, the twigs are no longer susceptible to the invasion of the fire blight organism.

2. That it is impracticable to attempt to cut out the blighted twigs during the growing season. The [illegible]

FIG. 12.—FORCING ROOTS BY "STRANGULATION"

Every variety so far tested in this manner springs roots readily. The nurse root was cut off at the constriction. Almost 50 varieties on their own roots are under experimentation.

of these twigs, since by the time external symptoms of the disease are evident to the fruit grower the bacteria have already migrated as far as they will go. The only possible advantage in cutting out blighted twigs is the removal of some of the sources of infection.

3. That it is a practical method of control to cut out the hold-over blight cankers during the **dormant season**, thereby removing the immediate sources of infection. One is never absolutely certain that the entire canker has been removed and this can be determined only by examination with the microscope to find how widely the bacteria have penetrated the tissues and formed cysts.

4. That under no conditions are crab apples of any variety recommended for root stocks. Every variety of crab apple so far investigated (and also the White Thorn or Crataegus species) have shown the encysted condition. French apple seedlings known to the nursery trade as "French Crab" have been found to be very susceptible to fire blight. It has been found that trees grown on "French Crab" up to five years of age have been killed in a single season (Fig. 7) by inoculating the roots with the fire blight organism. Fire blight has been isolated from the roots of trees grafted on French Crab stocks from the following counties of Pennsylvania (Figs. 2, 4, 8 and 9): Berks, Bucks, Centre, Chester, Erie, Franklin, Lackawanna, Lawrence, Lehigh, Luzerne, Mercer, Montgomery, and York.

5. That the final determination of what constitutes immunity to the attacks of the fire blight organism is best made by means of microscopic preparations.

FIG. 13.—USING SCIENCE IN TREE GROWING

Hundreds of trees on their own roots are being grown under controlled conditions in plots and in the greenhouses at The Pennsylvania State College for immunity studies.

(b) Problems

These investigations have indicated some problems whose solution is of fundamental importance in the finding of complete control measures.

1. There are indications that the encysted condition in hold-over cankers may occur more frequently in some varieties than in others. Possibly the encysted condition may never occur in some varieties. There is evidence that the encysted condition always develops in certain varieties. If varieties are resistant or immune to the encysting stage of the bacteria the problem of blight control is minimized or eliminated.

2. The outstanding difficulty of fire blight control is that a hold-over condition of some kind exists on the root system of the apple, through which the disease is perpetuated in the roots until too frequently death of the infected trees occurs (Figs. 4-9). It is impracticable to cut out root blight even in the dormant season due to the impossibility of its early recognition, since its presence is detected only by its effect on the tops.

3. The ultimate solution of the root blight problem is the propagation of resistant or immune varieties of apple on their own roots, and the growth of susceptible varieties on such immune root systems (Figs. 11-14). If they exist, such immune varieties propagated on their own roots will certainly solve one of the most serious phases of the fire blight problem. This is not such a laborious

FIG. 14.—NEW TREES FILL OPEN SPACES

In replanting the Grimes Golden Orchard of D. M. Wertz, Franklin County, Pennsylvania, 10 of the most promising varieties on their own roots were used in the experiment. Most of the trees in his orchard had died previously from collar and root blight.

task as at first may appear, nor will it take many years to determine the immune variety. Comparative resistance and immunity are determined by laboratory methods. The material to determine such immunity is already being accumulated. Fifty varieties of apples on their own roots are under experimentation (Fig. 13) and 1,200 trees of the most promising of these are planted in a region peculiarly favorable to the development of the root blight (Fig. 14). These trees are planted under practical orchard conditions with the coöperation of commercial growers to determine their adaptability (Fig. 14).

4. The genetical possibilities of the problem are not being neglected, for locked up somewhere in this investigation may be the key to the general problem of the inheritance of resistance and susceptibility. There can be no question that fire blight is especially favorable for the study of host and parasite relationships. That it may be possible to secure a high degree of resistance to the inroads of the disease or even total immunity to infection by the bacteria is indicated by

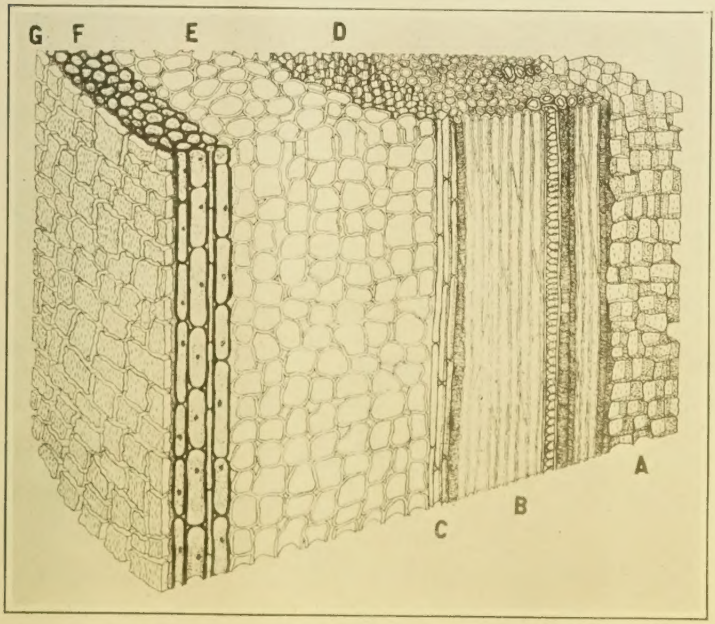

FIG. 15.—A SMALL BLOCK TAKEN FROM AN APPLE TWIG

A, the region of the pith. B, the wood which is the path of the soil moisture as it goes up the tree. C, the cambium or growing layer which is responsible for increasing the diameter. D, the phloem layer, the region through which plant foods travel downward from the leaves. E, the cortical region or storage region, which is the one most severely attacked by fire blight. G, the epidermis or protective layer. Drawing by J. Heist, student at The Pennsylvania State College.

the fact that there are wide degrees of resistance and susceptibility in the cultivated varieties of apple. The varieties most resistant to the disease are being self-pollinated and the seedlings grown for testing by means of the microscope following inoculation with the fire blight organism.

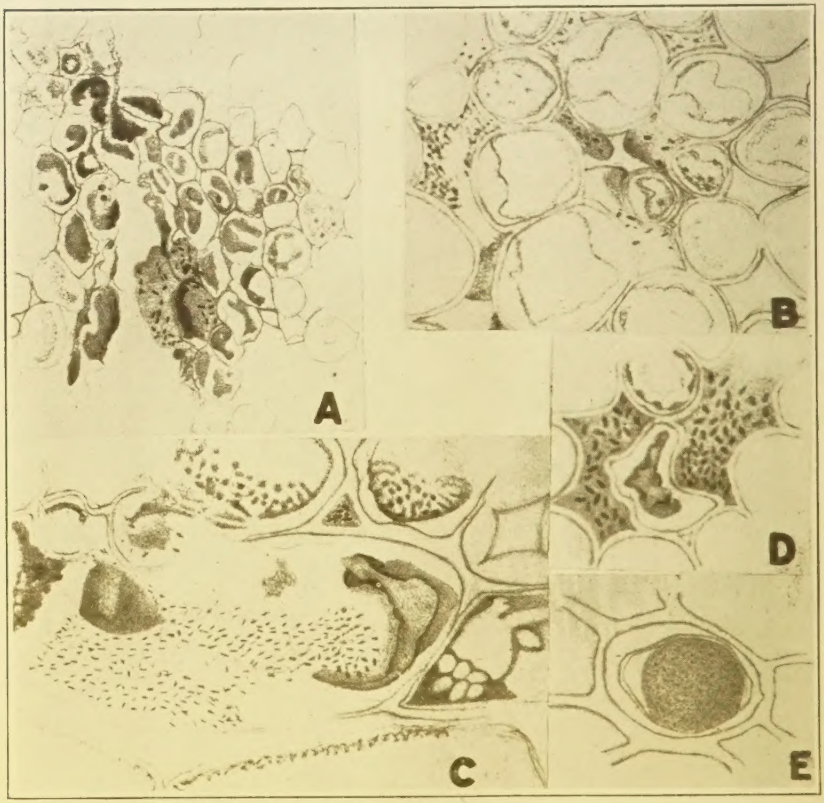

FIG. 16.—MICROSCOPE EXPOSES LIFE OF FIRE BLIGHT

A, a bacterial mass located at the margin of the puncture made by the needle in the inoculation. The bacteria extend from this point out into the uninjured tissue through the intercellular spaces as shown at B. The bacteria multiply rapidly in these spaces until cavities are formed from pressure and shriveling of the adjacent cells, as at D. Later a change takes place in the bacteria and they enter and destroy the living cell contents, as at C. Finally in the cell cavities the bacteria round up into a mass or cyst, which is the winter condition. These sections were taken from E of Fig. 15.